A SPATIAL AND TEMPORAL INVESTIGATION OF *ELEOCHARIS MACROSTACHYA* AND *ORCUTTIA TENUIS*

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Abstract

We investigated the possible spatial structure and temporal patterns that may determine the distribution and cover of *Eleocharis macrostachya* and *Orcuttia tenuis* within two vernal pools located in Tehama County, California. Rock cover, soil depth to hardpan, and basin elevation were compared with *E. macrostachya* and *O. tenuis* cover to investigate spatial structure. Yearly *E. macrostachya* and *O. tenuis* cover were compared with yearly precipitation and air temperature to assess temporal patterns.

The spatial results suggest that soil depth to hardpan may determine *E. macrostachya* distribution. Rock cover and basin elevation appeared to have little effect on either *E. macrostachya* or *O. tenuis* distribution.

Temporal analyses suggest that biotic interactions such as life history traits and competition may be important factors for *E. macrostachya* and *O. tenuis* distribution and density. *Orcuttia tenuis* cover is relatively stable at scale of 1.0 m² but varies at a 0.25 m². Variability at a micro scale could be due to variations in annual air temperatures causing a possible shifting mosaic steady state. *Orcuttia tenuis* life history traits coincide with adaptations expected for warmer temperatures.

Even though abundance is relatively stable for *O. tenuis* and *E. macrostachya* in both pools, there is significant negative correlation and spatial structure between them. *Eleocharis macrostachya* may dictate *O. tenuis* density within a pool through a combination of abiotic and biotic features.

Key Words: Competition, *Eleocharis macrostachya*, *Orcuttia tenuis*, shifting mosaic steady state, soil depth, Tehama County, vernal pools.

Changes in the distribution and density of populations over time and space provide the knowledge needed to understand the processes that regulate population size (Ricklefs 1997). Population parameters can be dictated by abiotic factors such as climate, topography, and soil depth, or biotic factors such as competition and life history traits. Understanding these processes is essential for the conservation and protection of vernal pool plants such as *Orcuttia tenuis* (CDFG 1991; USFWS 1997, 2003; CNPS 2001).

Vernal pools provide an excellent opportunity to explore species distribution and density in relation to abiotic processes and biotic interactions. Vernal pools are isolated wetlands with unique morphologies that fluctuate seasonally between periods of inundation and desiccation (Keeley and Zedler 1998). They support high levels of endemic species, both annual and perennials, and are considered a complex ecosystem (Holland and Dains 1990). The first reference to vernal pools and their distinctive plant associations can be attributed to Jepson (1925) and the large number of endemic species found within vernal pools to Hoover (1937). There are approximately 100 plants species commonly found in vernal pools, of which 90% are native and 55% endemic to California (Holland and Jain 1988; Keeler-Wolfe et al. 1998).

Vernal pools occupy areas of conflicting land use and have suffered extensive habitat destruction in the last century through urbanization and conversion to agriculture. California has lost between 93 and 97% of its vernal pools (Holland 1978). The continued destruction of vernal pool habitat has led to the designation of this unique ecosystem as "critical habitat" in 2003 by the United States Fish and Wildlife Service (USFWS). Due to the high level of endemism and the loss of critical habitat, there are 15 "listed" plants found in vernal pools, ten are listed as endangered, and five are threatened. *Orcuttia tenuis* A. Hitchc. (*Poaceae*), is a small, loosely tufted, blue-green annual, endemic to California vernal pools (Hickman 1993), which is listed by the State of California as threatened and

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by the federal government as endangered (CDFG 1991; USFWS 1997).

Alterations in hydrology can affect both abiotic processes and biotic interactions for vernal pool plants. The greatest threat to *O. tenuis* is altered hydrology (USFWS 2003), shorter inundation periods prevent *O. tenuis* seeds from dispersing and germinating (Corbin and Schoolcraft 1989). Seeds are distributed within the pools by floating as the pools fill in the rainy season (Crampton 1976) and require enough standing water to allow the growth of a soil fungus over the seed in order to break dormancy (Corbin and Schoolcraft 1989). This adaptation insures that *O. tenuis* will germinate only when sufficient water is present in the pool to complete its lifecycle. Likewise, longer inundation periods could have a detrimental affect by promoting the growth of a perennial marsh species, such as *Eleocharis macrostachya* Britton (Crampton 1959; Stone et al. 1988; Bauder 1989; Corbin and Schoolcraft 1989). Stone et al. (1988) reported that *E. macrostachya* competition combined with hydrological modification might have caused the loss of one *O. tenuis* population in Shasta County.

Inundation periods are affected by basin morphology (Brooks and Hayashi 2002), basin depth (Zedler 1987; Bauder 1987, 2000), soil (Griggs 1981; Holland and Dains 1990; Williamson et al. 2005), and yearly precipitation (Zedler 1987; Bauder 2000). The shape and size of a basin determines the amount of subsurface water-flow into the pools and deeper basins have longer inundation periods (Keeley and Zedler 1998). In general, soils act as reservoirs for the water and moisture retention varies with soil depth (Miller and Donahue 1990). Changes in any of these abiotic factors affect the inundation period of a pool, and hence the density and distribution of *O. tenuis*.

There is little information on the distribution of vernal pool plant species within an individual pool in relation to abiotic processes (basin morphology, basin elevation, and soil depth to hardpan) and biotic interactions (competition and life history traits). Our purpose is to gain information on the spatial structure and temporal patterns that affect *E. macrostachya* and *O. tenuis* distribution and density within individual vernal pools.

We aim to accept or reject the following hypotheses:

Spatial

1) *O. tenuis* and *E. macrostachya* have spatial structure and a significant negative correlation.
2) *O. tenuis* and *E. macrostachya* cover estimates have a significant positive correlation with decreasing basin elevation (deep depths).
3) *O. tenuis* cover estimates have a significant positive correlation with decreasing soil depth to hardpan and increasing rock cover.
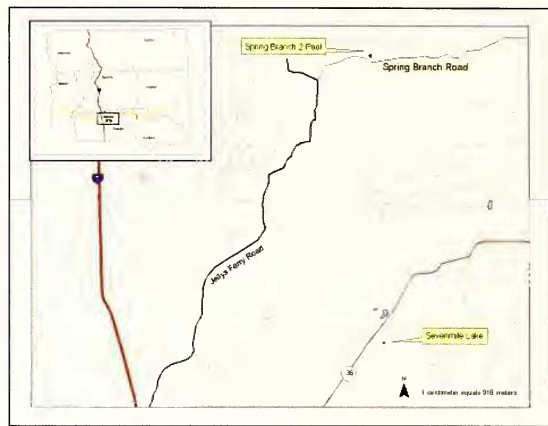

FIG. 1. Location of study pools in eastern Tehama County, California.

4) *E. macrostachya* cover estimates have a significant positive correlation with increasing soil depth to hardpan and decreasing rock cover.

Temporal

1) *O. tenuis* and *E. macrostachya* cover estimates vary significantly over sampling years at both a 0.25 m² and 1.0 m² scale.
2) *O. tenuis* and *E. macrostachya* cover estimates have a positive correlation with increasing precipitation and decreasing air temperatures.

The results from these tested hypothesizes will guide management of *O. tenuis* through the identification of critical abiotic and biotic habitat preferences.

METHODS

Study Area

Two large deep northern volcanic vernal pools were surveyed in the Northeastern Sacramento Valley Vernal Pool Region (Keeler-Wolfe et al. 1998). The first pool sampled, Sevenmile Lake (7-Mile) is owned and managed by the Bureau of Land Management (BLM) and is located approximately seven miles northeast of Red Bluff on Highway 36 (Fig. 1). Sevenmile Lake is approximately 2.3 acres. The second pool is Spring Branch 2 (SB2), also owned by BLM, located on Spring Branch Road and is approximately 3.32 acres in size (Fig. 1). Resource and geographic constraints limited this study to only two vernal pools.

Data Collection

All data points were recorded with a Trimble GeoExplorer 3 GPS unit, differentially corrected,

and exported to a resident ArcGIS shapefile format.

Basin morphology. The perimeter of each pool was walked with a Trimble GPS unit and delineated by the lack of common shallow water wetland and vernal pool indicator species typical in these pools. In low gradient areas with more widely fluctuating inundation periods, the species most often used for delineation were *Deschampsia danthonioides*, *Hordeum marinum* ssp. *gussoneanum*, and in some areas, *Lolium multiflorum*. In higher gradient areas with more stable long inundation periods, typical species were *Eryngium castrense*, *Downingia* spp., *Eleocharis macrostachya*, and *Orcuttia tenuis*. Hydrologic and geomorphologic features also were used extensively.

Basin elevation. A laser level (Topcon RL-H3C 980′ Diameter- Servo Leveling) was used to map the basin elevation of the vernal pool basins in Fall 2005. Line transects were placed every ten meters, running in a general east to west pattern through the vernal pool basin and elevation points were collected every five meters along each transect. A total of 253 elevation points were collected along ten transects for 7-Mile and 268 elevation points were collected along 16 transects for SB2. Additional elevation points were collected in the upland mosaic to create a more accurate physiographic map.

Relative cover estimates. Rock, *E. macrostachya*, and *O. tenuis* cover were estimated every five meters along the basin transects. Cover was determined by using two 0.5 m^2 quadrats placed side by side at each elevation point, and was read as one meter squared. A modified cover class system was created and used to quantify cover estimates in this study (Table 1). A total of 1601 m^2 quadrats were read for 7-Mile in October 2005 and 3001 m^2 quadrats were read for SB2 in July 2006.

Soil depth to hardpan. The measurable depth of soil to hardpan was calculated using a soil probe at the same location and time as the vegetation quadrats within the basin. At this time the pool soils were completely dry and usually cracking due to desiccation. The soil probe was pushed into the ground, usually between three and seven times, within each 1 m quadrat. Each time the soil probe was pushed into the basin floor; the ground surface level was marked and measured to the end of the probe. The maximum soil depth was recorded in centimeters for each vegetation sampling point.

Absolute cover estimates. As part of an earlier vernal pool study, permanent transects were established in 1999 from a stake (pivotal point) driven into a central area of a pool that traverses

TABLE 1. *ORCUTTIA TENUIS* AND *E. MACROSTACHYA* ESTIMATE RELATIVE COVER CLASSES.

Class	Percent Cover
0	Absent
1	1–10%
2	11–20%
3	21–30%
4	31–40%
5	41–50%
6	51–60%
7	61–70%
8	71–80%
9	81–90%
10	91–100%

to the pool margin (Lis and Eggeman 1999; Lis and Clark 2007). Sevenmile Lake has four transects and SB2 has two transects. A system of permanently marked quadrats, located on permanent transects was used with the permanent quadrats and transects marked with large steel spikes. At each spike, four quadrats (0.25 m^2) were laid out, and the absolute cover of rock, bare ground, and indicator plant species recorded, including *O. tenuis* and *E. macrostachya*. Data were collected in the years 1999, 2000, 2001, 2004, and 2006.

Climate data. The mean maximum monthly air temperature and mean monthly precipitation data were obtained from the California Department of Water Resources (DWR) (http://cdec.water.ca.gov/queryTools.html) and Western Regional Climate Data Center (http://www.wrcc.dri.edu/). The data station used was Red Bluff Diversion Dam (RBD) for both queries.

Data Analysis

Basin morphology. The area and perimeter of each pool was automatically calculated during the creation of the polygon shapefile. The shape value was calculated using the following equation: perimeter/(3.54 * sqrt (area)), where the value of 1.0 is equal to a circle, and larger for a distended shape (Longley et al. 2001).

Basin elevation and soil depth to hardpan. The elevation points were interpolated into a Digital Elevation Model (DEM), using Hutchinson's (1989) Topo to Raster implemented in ArcGIS Ver. 9.1 (Environmental Systems Research Institute), which interpolates a hydrologically correct surface from point, line, and polygon data. A two-group t-test was performed between the two pools to determine the significant difference between means for soil depth to hardpan and basin elevation.

Spatial autocorrelation. Spatial dependence in *O. tenuis* and *E. macrostachya* was investigated in

several ways to understand both the overall spatial pattern of each species (global random vs. non-random structure) and to identify significant patch distributions in each pool. These tests also helped us to anticipate any issues with conducting standard normal linear statistics. While spatial autocorrelation does not inflate the explained variance term (in r or r^2 relationship analysis), it can lead to inflated (artificially large) sample sizes due to non-independent samples, which may influence significance tests (P-values) and result in the inclusion of non-significant predictor variables (Legendre and Fortin 1989). The local spatial correlation was examined using isotropic derived Moran's I correlograms and local indicators of spatial association (LISA) maps (Anselin 1995).

Correlations. After spatial autocorrelation was examined, the point shapefiles representing cover estimates and soil data for each site were buffered by 1 m to create a 1 m diam. zone for each point and zonal statistics were calculated from the DEM. The zonal statistical result (the mean basin elevation) was added to the field data (soil depth to hardpan and cover estimates) to create a data analysis matrix for each pool. All statistical tests were performed in Systat 8.03 (SPSS Inc.) with α ≤ 0.05.

Since the cover estimates were ranked data, a Spearman's rank correlation matrix was used to determine if there was a significant correlation between *O. tenuis* and *E. macrostachya* with rock, soil depth, and elevation (Sokal and Rohlf 1981). Linear regressions were calculated in order to determine variable predictability.

Absolute cover estimates. Analyses of absolute cover estimates were conducted at two scales. The first scale was at the 0.25 m² level for which each of the four quadrats per sampling point were individually analyzed to examine micro-changes in distribution within the pool. The second scale was at 1.0 m² for which each of the four quadrats per sampling point were averaged to aggregate the data into one sampling point value to examine changes at the whole pool level.

A one-way Analysis of Variance (ANOVA) was used at both scales (0.25 m² and 1.0 m²) to determine if there was a significance difference in mean absolute cover estimates for *O. tenuis* and *E. macrostachya* over sampling years. A Boneferroni post-hoc comparison was used to determine significant differences among years.

Climate data. Air temperature and precipitation data were tested against *O. tenuis* and *E. macrostachya* cover using a Pearson's Correlation Test (α ≤ 0.05). Data were checked for normality before analysis and linear regressions were used to determine if air temperature and precipitation were significantly correlated.

TABLE 2. COMPARISON OF BASIN MORPHOLOGY (AREA, PERIMETER, AND SHAPE) FOR EACH VERNAL POOL.

Sevenmile Lake	Spring Branch 2 Pool
Area = 9460 m²	Area = 13,838 m²
Perimeter = 479 m	Perimeter = 440 m
Shape = 1.15	Shape = 1.27

RESULTS AND DISCUSSION

Spatial Data

Basin morphology. Spring Branch 2 pool is the larger pool with a distended shape that has been caused by an artificial dirt dam on the southwest side of the pool (Table 2). It has been suggested that artificial dirt dams provide more area suitable for *Orcuttia* growth by prolonging inundation (Griggs 1974).

Basin elevation and soil depth to hardpan. In addition to SB2 being larger than 7-Mile, it is deeper with less soil. T-tests determined a significant difference between means (7-Mile = 0.72 ft and SB2 = 1.16 ft) for basin elevation (df = 458, P = 0.000) and between means (7-Mile = 8.62 cm and SB2 = 6.79 cm) for soil depth to hardpan (df = 458, P = 0.002) between the two pools. Since the study pools are morphologically different, *O. tenuis* and *E. macrostachya* distribution and cover may vary between pools due to microhabitat differences.

Spatial autocorrelation. One of our larger goals was to determine if there is significant spatial structure for *O. tenuis* and *E. macrostachya* within the study pools. The value for Moran's I for global spatial autocorrelation indicate that spatial pattern of *O. tenuis* and *E. macrostachya* are not random but have significantly clustered patches in both pools (P = 0.01).

Moran's I correlograms also detected spatial structure in the populations between pools. If cover diversity were randomly distributed, the correlograms would be statistically non-significant and would exhibit a more or less flat profiles (values near 0 for most distance classes). The Moran's I correlograms (Fig. 2) show *O. tenuis* and *E. macrostachya* have significant positive autocorrelation detected in the pool at different distances depending on the pool. The spatial autocorrelation pattern (size of patches) for *E. macrostachya* is different (7-Mile = 0–52 m, SB2 = 0–32 m), and *O. tenuis* is similar (7-Mile = 0–45 m, SB2 = 0–51 m), between study pools (Fig. 2).

The distance differences for significant positive spatial autocorrelation detected for *E. macrostachya* in 7-mi compared SB2 could be due to pool abiotic differences (soil depth to hardpan) and/or biotic differences (life history reproduction) (Sokal and Oden 1978). *Eleocharis macro-*
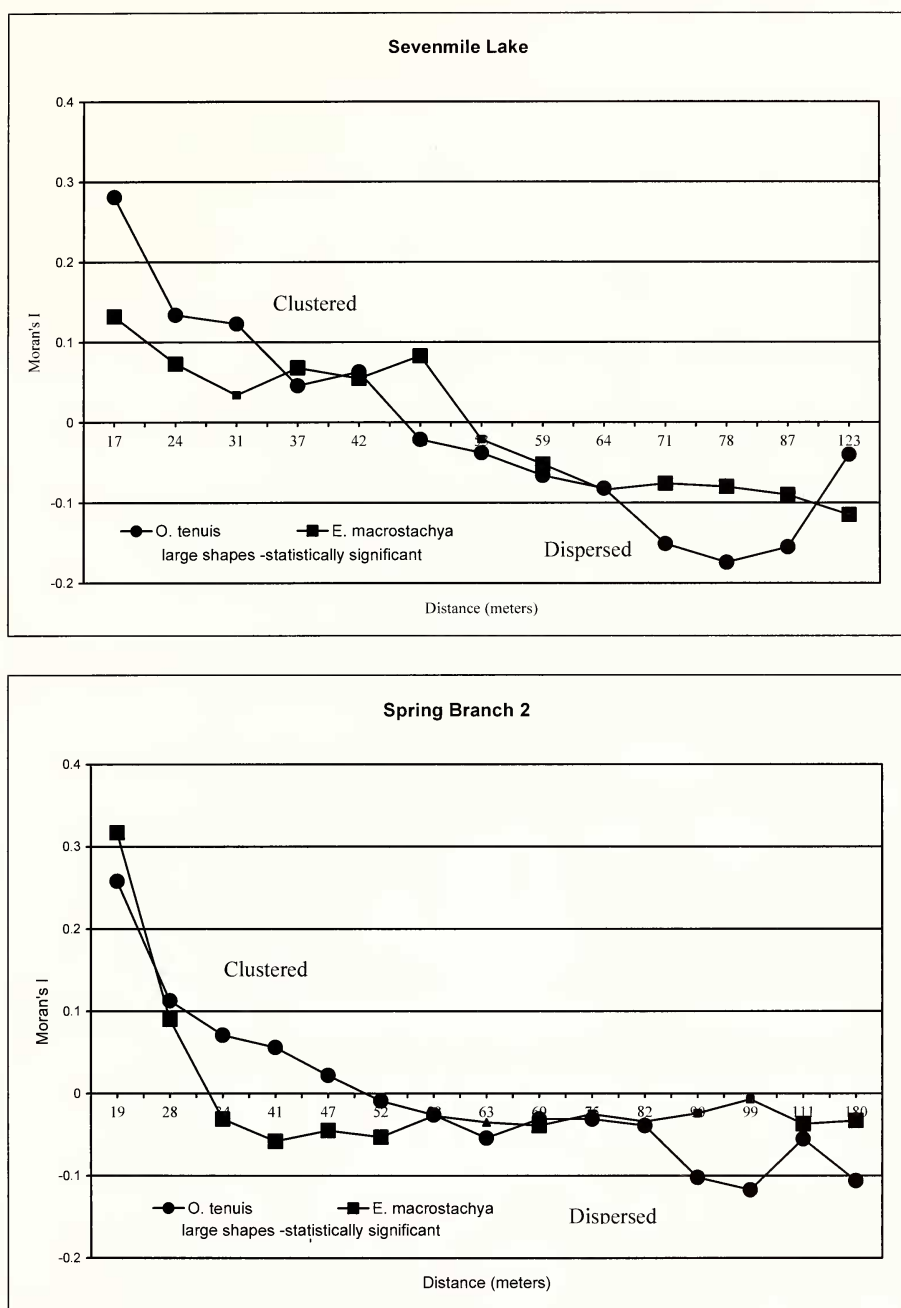
FIG. 2.   A correlogram for *O. tenuis* and *E. macrostachya* in Sevenmile Lake and Spring Branch 2 Pool.

stachya is perennial and reproduces vegetatively from rhizomes and by seeds (DiTomaso and Healy 2003). Seeds typically germinate in standing water during mid-spring through early summer (DiTomaso and Healy 2003) and rapid rhizomatous growth occurs in mid and late summer (Strandhede 1966). *Orcuttia tenuis* is an annual, and only reproduces by seeds, which are distributed within the pools by floating as the pools fill in the fall or winter (Crampton 1976).

Because vegetative reproduction is not observed in *O. tenuis*, this autocorrelation at similar distance classes probably reflects the occurrence of similar patch area sizes (i.e., high probability areas for survival) for plant development in this annual.

According to Sokal (1979), patch size can be estimated by the distance at which the Moran's I correlogram first intercepts the abscissa, as this corresponds to the shortest dimension of an

irregularly shaped patch. The Moran's I correlograms (Fig. 2) also indicate that there is a linear gradient from significant to non-significant autocorrelation across each pool for both species (i.e., positive values are not seen at higher distance classes). This suggests there is not a circular gradient (Sokal and Oden 1978) of patches for these species in a pool (i.e., not like a typical vernal pool bathtub ring of species distribution) and that the patch distribution is not regular (Legendre and Fortin 1989; Radeloff et al. 2000). Figures 3 and 4 show the location of significant clusters of *E. macrostachya* and *O. tenuis* within the pools in relation to rock cover, soil depth, and basin elevations.

Biotic correlations. A Spearman's rank correlation matrix determined that *O. tenuis* and *E. macrostachya* clusters are significantly negatively correlated in both pools (7-Mile P = 0.00; SB2 P = 0.00; Figs. 4 and 5). A linear regression found a negative significant correlation between *O. tenuis* and *E. macrostachya* in both pools but that is a weak predictor for cover (7-Mile – df = 157, adjusted r^2 = 0.18, P = 0.00 and SB2 – df = 297, adjusted r^2 = 0.13, P = 0.00). This result suggests that there is a better predictor variable for cover such as inundation period, which was not examined in this study. Even though the negative correlation between the species is weak, the relationship may be competition, which is supported by Stone et al. (1988), who observed that competition with *E. macrostachya* rather than inundation directly limits the distribution of *O. tenuis*.

Abiotic correlations – Orcuttia tenuis. Basin elevation.—A Spearman's rank correlation matrix determined that the 7-Mile population of *O. tenuis* is significantly negatively correlated (df = 155, P = 0.00) with basin elevation. A 7-Mile LISA map of *O. tenuis* cover and basin elevation shows that the significant patches of *O. tenuis* are found in shallower depths of the pool (Fig. 3). A linear regression found basin elevation to be a weak but significant predicting variable (df = 157, adjusted r^2 = 0.18, P = 0.00). This result also suggests that another variable such as inundation period may be a better predictor for *O. tenuis* cover.

A Spearman's rank correlation matrix determined that the SB2 population of *O. tenuis* had no significant correlation (df = 295, P = 0.24) with basin elevation. The lack of correlation between *O. tenuis* cover and basin elevation can be seen in the location of the significant patches of *O. tenuis* on the SB2 LISA map (Fig. 4). The significant clusters of *O. tenuis* were not found at shallow or deep depths in SB2 and suggest basin elevation does not affect *O. tenuis* density and distribution.

The lack of positive correlations between *O. tenuis* cover and basin elevation is unexpected because previous research indicates *O. tenuis*

prefers deep portions of a pool (Corbin and Schoolcraft 1989), but not surprising since we observed *O. tenuis* patches in the shallow and medium depths of the pools. This result could be due to the large size of the study pools, which tend to have longer inundation periods (Brooks and Hayashi 2002). The deep portions of the study pools may have an exceptionally long inundation period that push *O. tenuis* to survive in the shallow and medium depths of the pool. These shallower depths must have an inundation period long enough to meet the threshold of *O. tenuis* (Holland 1987). Our findings may indicate that inundation period not depth affect *O. tenuis* abundance and distribution.

Rock cover and soil depth to hardpan.—A Spearman's rank correlation matrix found that *O. tenuis* has a significant positive correlation (7-Mile df = 155, P = 0.00; SB2 df = 295 P = 0.00) with rock and no significant correlation (7-Mile df = 155, P = 0.69; SB2 df = 295, P = 0.53) with soil depth to hardpan in both study pools. For SB2, a linear regression analysis found rock cover to be an insignificant predicting variable for *O. tenuis* cover. Rock cover may shape *O. tenuis* distribution within a pool by allowing more available microhabitat for *O. tenuis* that may not be suitable for other vernal pool plant species. Soil depth to hardpan appears to have little to no affect on *O. tenuis* distribution and abundance. Research on soil requirements for *O. tenuis* is not currently available indicating a need for more information.

Abiotic correlations – Eleocharis macrostachya. Basin elevation.—A Spearman's rank correlation matrix found *E. macrostachya* to have no significant correlations (7-Mile df = 155, P = 0.89; SB2 df = 295, P = 0.68) with basin elevation in both study pools. The locations of significant *E. macrostachya* clusters in relation to elevation show this lack of correlation (Figs. 3 and 4). In these LISA maps, it appears the significant patches of *E. macrostachya* were not found in shallow or deep depths for both study pools. These results suggest that the inundation requirements for *E. macrostachya* are being met across the topographic gradient, which are standing water no deeper than 1 m with occasional fluctuations down to saturated conditions throughout the growing season (USDA 2006).

Rock cover and soil depth to hardpan.—A Spearman's rank correlation matrix found *E. macrostachya* has a significant negative correlation (df = 295, P = 0.00) with rock cover and significant positive correlation (df = 295, P = 0.00) with soil depth to hardpan in SB2. There is a significant negative correlation between soil and rock cover indicating that rock cover probably has little affect on *E. macrostachya* and was eliminated from the linear regression, which
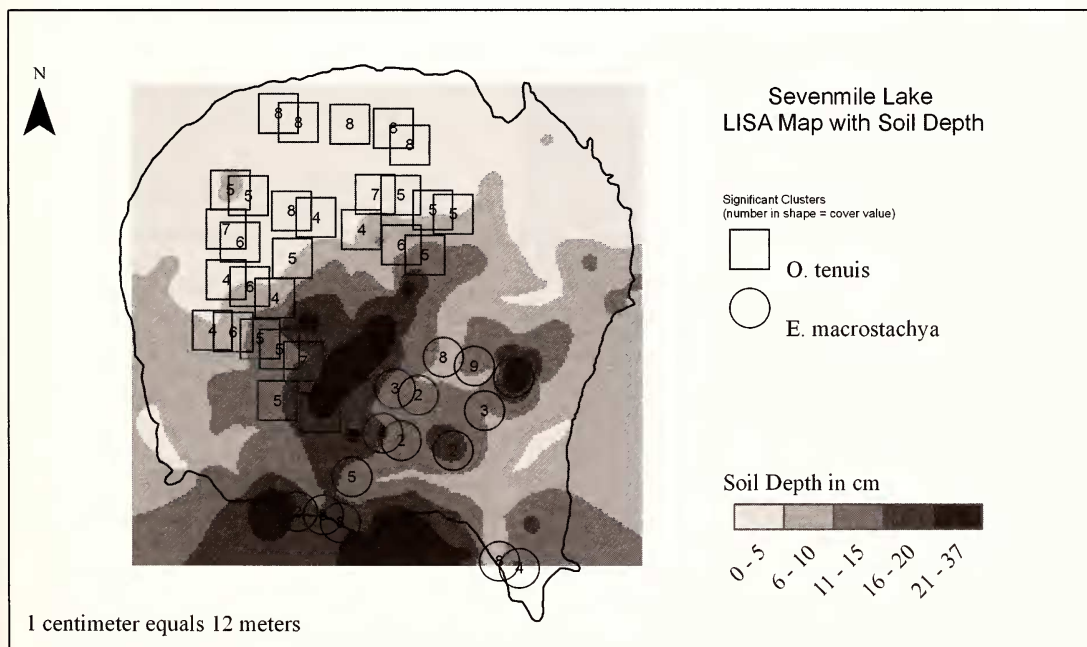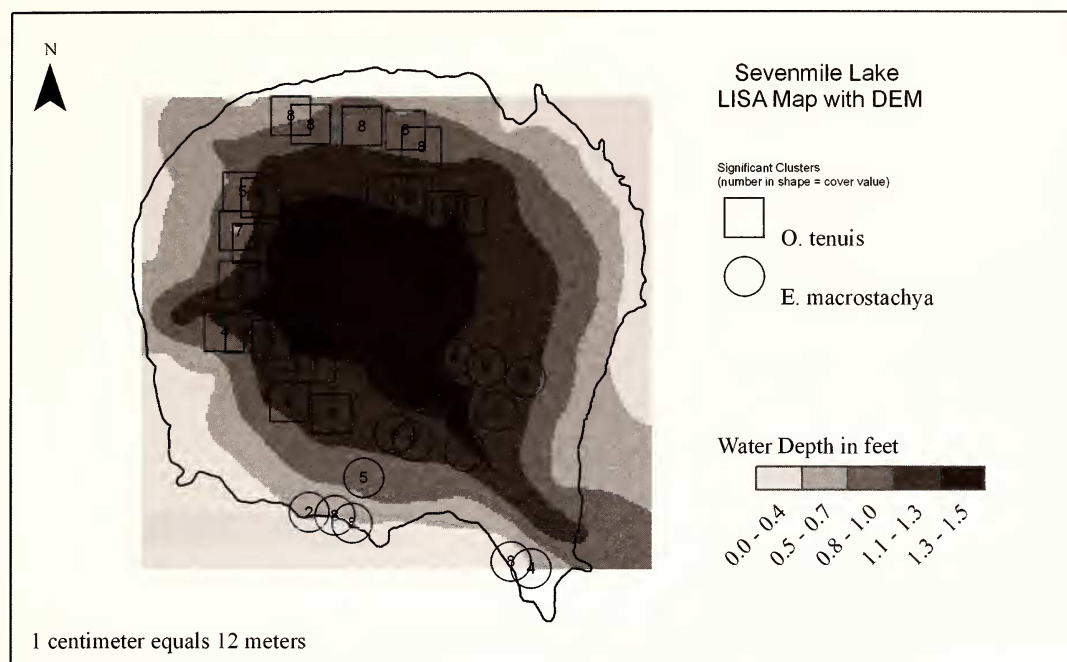
FIG. 3.   A LISA map of significant *O. tenuis*, *E. macrostachya* patches in Sevenmile Lake in relation to basin elevation and soil depth. *Orcuttia tenuis* has a significant negative correlation with *E. macrostachya* and basin elevation. *Eleocharis macrostachya* has a significant positive correlation with soil depth to hardpan.

found soil depth to be a significant (df = 297, adjusted r² = 0.23, P = 0.00), but weak predicting variable for *E. macrostachya* cover. This result suggests that another variable such as inundation period may be a better predictor for *E. macro-stachya* cover. In 7-Mile and SB2, a Spearman's rank correlation matrix found *E. macrostachya* has a significant positive correlation (df = 295,
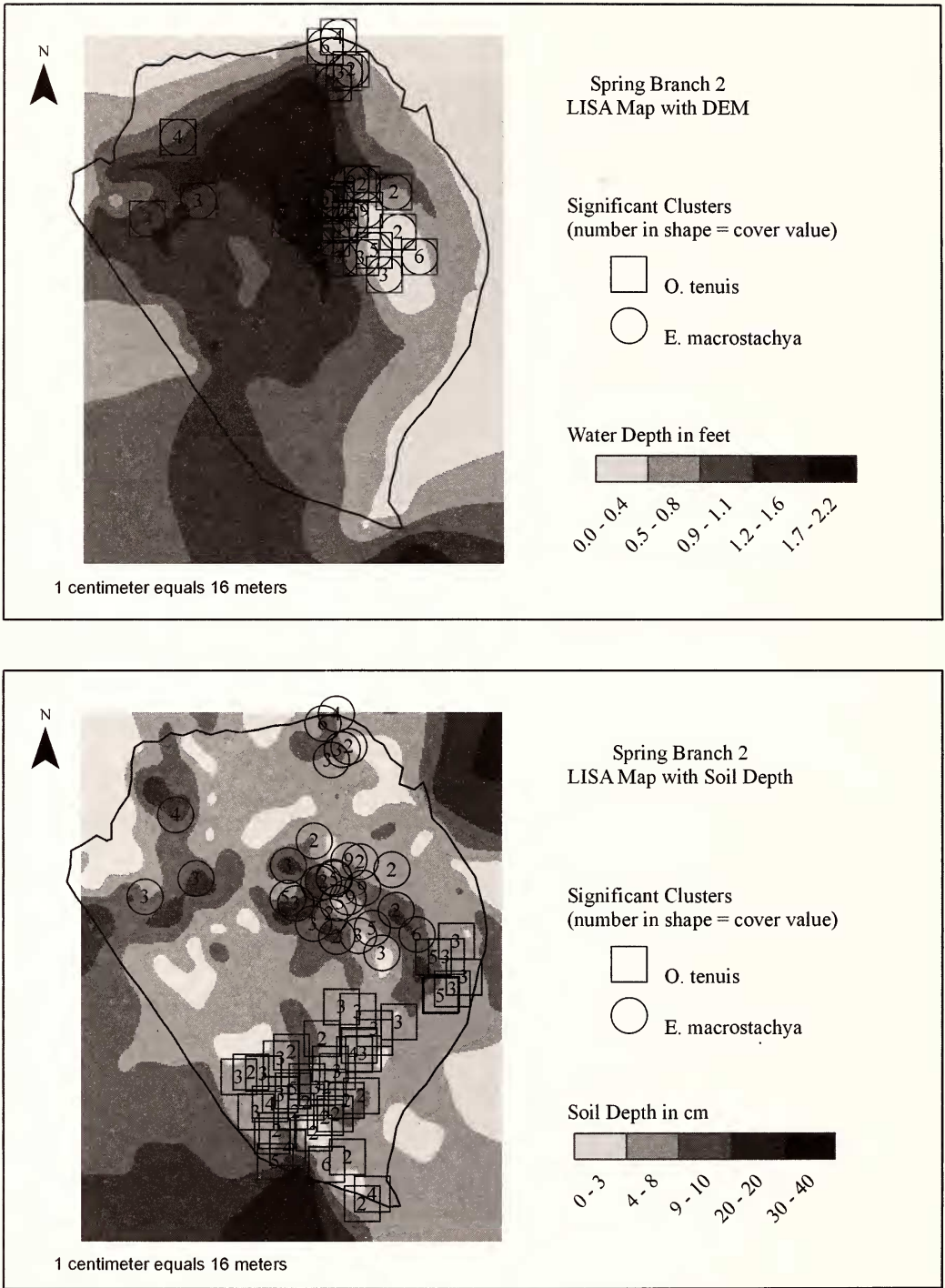
Fig. 4.   A LISA map of significant *O. tenuis*, *E. macrostachya* patches in Spring Branch 2 Pool in relation to basin elevation and soil depth. *Orcuttia tenuis* has a significant negative correlation with *E. macrostachya* and no correlation with basin elevation. *Eleocharis macrostachya* has a significant positive correlation with soil depth to hardpan.

P = 0.00) with soil depth and no correlation with rock. The positive soil correlation can be seen in a LISA map of each pool, representing the significant patches of *E. macrostachya* in relation

to soil depth to hardpan (Figs. 3 and 4). These results suggest that soil depth to hardpan may determine *E. macrostachya* density and distribution in both study pools.

Sevenmile Lake
Least Squares Means
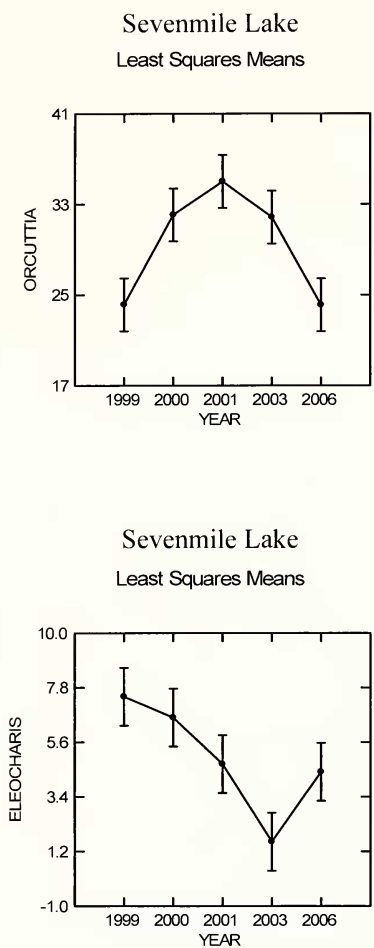

Sevenmile Lake
Least Squares Means

FIG. 5. The mean absolute cover of *O. tenuis* and *E. macrostachya* (0.25 m²) in Sevenmile Lake and over sampling years.

The positive correlation between *E. macrostachya* and soil depth to hardpan, may explain why *E. macrostachya* patches were larger in SB2 compared to 7-Mile (Figs. 3 and 4). Spring Branch 2 pool has a greater mean for soil depth to hardpan compared to 7-Mile, indicating soil depth may determine cluster size. Soil depth to hardpan may play an important part in the significant spatial structure of *E. macrostachya* and *O. tenuis* in both study pools.

Temporal Data

Absolute cover estimates. A one-way ANOVA found a significant difference in mean absolute cover estimates for *O. tenuis* and *E. macrostachya* over sampling years for 7-Mile, at the micro scale of 0.25 m² (df = 315, *O. tenuis* P = 0.00; *E. macrostachya* P = 0.01). The mean absolute cover of the 7-Mile population of *O. tenuis* is significantly different between 1999 and 2001 (df = 315, P = 0.01), and 2001 and 2006 (df = 315, P = 0.01), 2001 having the highest mean (Fig. 5). The mean absolute cover of the 7-Mile population of *E. macrostachya* at the micro scale of 0.25 m² is significantly different between 1999 and 2003 (df = 315, P = 0.01), and 2000 and 2003 (df = 315, P = 0.03), with 1999 having the highest mean and 2003 the lowest (Fig. 5).

In SB2, *O. tenuis* cover also varied at micro scale (0.25 m²) over sampling years. A one-way ANOVA found a significant difference (df = 155, P = 0.01) in mean absolute cover estimates for *O. tenuis* is significantly different between 1999 and 2000 (df = 155, P = 0.03), 2000 and 2003 (df = 155, P = 0.01), and 2000 and 2006 (df = 155, P = 0.02), with 2000 having the highest mean (Fig. 6). There is no significant difference (df = 155, P = 0.96) in mean absolute cover estimates at a micro scale (0.25 m²) for *E. macrostachya* over sampling years in SB2 (Fig. 6).

These results indicate that *O. tenuis* mean absolute cover at a 0.25 m² scale changes over time. Sevenmile Lake and SB2 have different years for high cover estimates of *O. tenuis*, which could be caused by morphological differences between the pools.

Since *E. macrostachya* cover only varied in 7-Mile, these results indicate *E. macrostachya* may be relatively stable over time. *Eleocharis macrostachya* cover may have varied over sampling years in 7-Mile and not SB2 because of soil depth differences between the pools. Sevenmile Lake has a higher mean for soil depth to hardpan compared to SB2, which may allow for more variability in density and distribution for *E. macrostachya*.

A one-way ANOVA found no significant difference in mean absolute cover estimates for *O. tenuis* and *E. macrostachya* over sampling years for both study pools at an aggregated 1.0 m² scale. This result is puzzling since *O. tenuis* cover varied at a 0.25 m² scale and unexpected because research has shown that climate (Crampton 1959; Griggs 1976, 1981; Griggs and Jain 1983) and possible competition between *E. macrostachya* and *O. tenuis* (Crampton 1959; Stone et al. 1988) limited *O. tenuis* abundance. Our results suggest that *E. macrostachya* and *O. tenuis* cover is relatively stable at the whole pool level.

Even though *O. tenuis* cover is relatively stable at a 1.0 m² scale, changes on a micro scale (0.25 m²) indicate a possible "shifting mosaic steady state". Bormann and Likens (1979) report "shifting mosaic steady state" is the result of yearly disturbances changing the location for a specific habitat, however, even though the actual locations change, the amount of each habitat over a large area may remain somewhat constant (steady state). Disturbances cause changes in habitat. Yearly changes in precipitation and air temperature, hence weather, may affect *O. tenuis* cover.
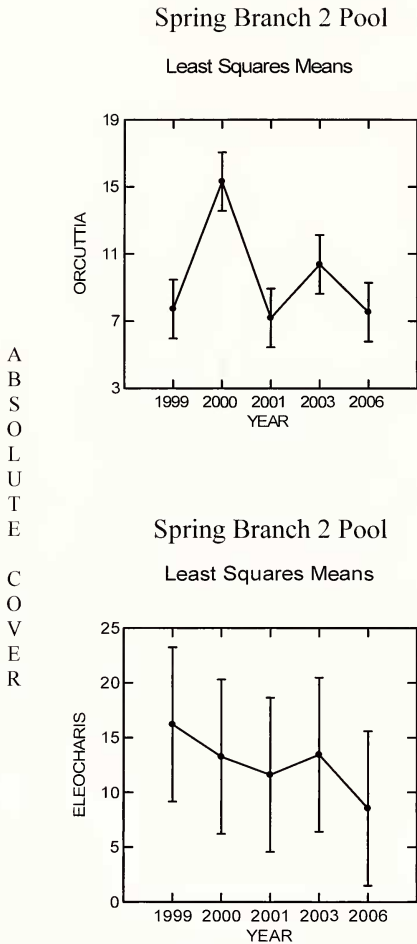
Spring Branch 2 Pool

Least Squares Means

Spring Branch 2 Pool

Least Squares Means

Fig. 6. The mean absolute cover of *O. tenuis* and *E. macrostachya* (0.25 m²) in Spring Branch 2 over sampling years.

Climate data. Eleocharis macrostachya and *O. tenuis* mean absolute cover at a 0.25 m² scale changes over time, and may be due to changes in weather. A Pearson's correlation matrix determined that there is a significant positive correlation (df = 109, P = 0.02) between air temperature and *O. tenuis*, and a significant negative correlation (df = 109, P = 0.02) between precipitation and *E. macrostachya* at the 0.25 m² scale within 7-Mile. A linear regression (df = 109, adjusted r^2 = 0.03) for *O. tenuis* mean absolute cover found precipitation (P = 0.01) to be a negative predicting variable and (P = 0.00) air temperature a positive predicting variable, with air temperature as the stronger predictor. For *E. macrostachya* mean absolute cover, a linear regression (df = 109, adjusted r^2 = 0.02, P = 0.02) determined precipitation is the only significant predicting variable.

In SB2, a Pearson's correlation matrix found a significant positive correlation (df = 158, P =

0.05) between *O. tenuis* and air temperature. A linear regression (df = 158, adjusted r^2 = 0.02, P = 0.05) determined that air temperature is a significant but a weak predictor for *O. tenuis* cover. No climate correlations were found for *E. macrostachya* cover in SB2. This result is anticipated since *E. macrostachya* cover did not vary over time in SB2.

Our results suggest that *O. tenuis* cover is not affected by the amount of rain per year, which is unexpected based on previous studies suggesting there is relationship between precipitation and *O. tenuis* (Crampton 1959; Griggs 1974, 1981; Griggs and Jain 1983). The differences in correlation between *O. tenuis* and precipitation could be related to the differences in correlation with basin elevation, since basin elevation (Zedler 1987; Bauder 1987, 2000) and yearly precipitation (Zedler 1987; Bauder 2000) are connected to the inundation period of a vernal pool. The study pools are large and deep which promote long inundation periods (Brooks and Hayashi 2002). These longer inundation periods may meet the inundation threshold for *O. tenuis* seeds (Reeder 1965, 1982; Holland 1987) across the topographic gradient, indicating that duration not depth of inundation determine *O. tenuis* distribution.

The positive correlation between *O. tenuis* cover and air temperature suggests that cover will be higher in warmer years and possibly due to the ability of *O. tenuis to* switch from a C-3 to C-4 photosynthesis in the late spring (Corbin and Schoolcraft 1989). This switch to C-4 photosynthesis allows *O. tenuis* to adapt to high intensive sunlight and use water more efficiently. This may also explain why *O. tenuis* significant clusters were not found in the deep parts of the pools. If a winter season extends into late spring, the lack of sunlight and increased precipitation will hinder the C-4 photosynthesis pathway of *O. tenuis*, especially in deep parts of the pool. In this situation, *O. tenuis* cover will be higher in shallower depths further supporting a hypothesis for shifting mosaic steady state (Bormann and Likens 1979).

Conclusions

It is important to understand the abiotic and biotic features that limit the distribution and density of a species, especially for species and habitats that have a special conservation status, such as *O. tenuis* and vernal pools.

Eleocharis macrostachya and *O. tenuis* abundance is relatively stable in both pools at a 1 m² scale. *Orcuttia tenuis* cover varied over time in both pools at the 0.25 m² scale, which could be due to a combination of biotic (negative correlation with *E. macrostachya* and life history reproduction traits) and abiotic (positive correla-

tion with air temperature) features. It is important to emphasize that although cover changes occur at a micro scale these changes were not reflected when the data were aggregated at a scale of 1.0 m². Annual changes in air temperatures that allow *O. tenuis* to thrive in some areas of the pool better than others in different years may be explained by the shifting mosaic steady state theory.

Although cover is relatively stable in both pools for *O. tenuis* and *E. macrostachya* at the 1.0 m scale, we found both a significant negative correlation between the two species. Temporal data show no significant changes in cover over time for both *E. macrostachya* and *O. tenuis* at a 1 m² scale. Thus, if competition is occurring between *E. macrostachya* and *O. tenuis*, *E. macrostachya* is not limiting the density of *O. tenuis* but rather dictating its distribution within a pool. Our data show that depth of soil to hardpan may drive *E. macrostachya* density and distribution. *Eleocharis macrostachya* is perennial species that thrives in pool areas with deep soils (soil depth >6 cm), which can prevent *O. tenuis* from establishing in these areas. Since *O. tenuis* cannot establish in areas with *E. macrostachya*, it is forced to live in the rocky areas of a pool that have shallow soils.

Our results show that conservation strategies need to include monitoring sedimentation within the vernal pools by managing grazing activities and limiting anthropogenic disturbances that may increase erosion in the surrounding uplands. If pools fill with sediment, it will increase the available habitat for *E. macrostachya*; hence limit available habitat for *O. tenuis*.

Our results show that soil plays an important role in conserving vernal pool plant species. Future research for *O. tenuis* conservation should include soil mapping, transplant experiments, and inundation periods. Mapping soils based on texture and chemistry may give insight on the soil types preferred by *E. macrostachya* and *O. tenuis*. Conducting transplant experiments in different soil depths would determine if there is positive correlation between of soil depth and possible completion between *E. macrostachya* and *O. tenuis*.

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